The Theory of Ancestral Contributions in Heredity.

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(Received March 19,—Read April 22, 1909.)

Under the above title a paper has recently appeared by Mr. A. D. Darbishire in the 'Roy. Soc. Proc.,' vol. 81, B, p. 61 *et seq.*, giving further experimental evidence with regard to the inheritance of certain characters in peas. The paper is an interesting one, but the method adopted is not, I venture to think, capable of answering the problem which the author set himself. It has been supposed by some Mendelians that the theory of inheritance summed up in the "law of ancestral heredity" was in some way invalidated by investigations such as Mr. Darbishire's, and that opinion consciously or unconsciously seems to be expressed in the paper just referred to. The law of ancestral heredity is embraced in the following statements:—

(i) In a population breeding without assortative mating the regression line for offspring on any ancestor is linear.

(ii) The correlations between offspring and the successive grades of ancestry form a progression diminishing geometrically as we ascend to distant grades; and

(iii) The general relation of an individual to his ancestry can be closely expressed by the multiple correlation formula.

In a memoir published in the 'Phil. Trans.,' vol. 203, pp. 53–86, I showed that these principles held for material obeying Mendel's laws—in particular (i) and (ii) hold for the simple case of alternative characters such as are said to occur in the case of peas.

The only instance that I am aware of in which ancestry does not matter is that in which the geometrical progression is of the form:

$$\rho, \rho^2, \rho^3, \ldots.$$

I treated this case at length in the 'Phil. Trans.,' vol. 187, A, pp. 304–6 (1896), remarking that the grandparents were quite indifferent, when the parents had been selected. Unfortunately, this is not true when the correlation coefficients are

$$\frac{1}{3}, \frac{1}{2}\times\frac{1}{3}, \frac{1}{2^2}\times\frac{1}{3}, \frac{1}{2^3}\times\frac{1}{3}, \text{ etc.,}$$

as is the case with the somatic correlations on the Mendelian theory. In other words, ancestry does matter in the latter theory. What is the explanation, therefore, of the apparent contradiction between such experiments as those of Mr. Darbishire and the theoretical development of the Mendelism which they profess to establish ?

It does not seem hard to account for the divergence. Experiments such as those of Mr. Darbishire do not deal with a population as a whole, and consider the contributions to the next generation of all its components supposed to be mated at random. I feel quite certain that if Mr. Darbishire makes the requisite crosses in due proportions, and does not weight with differential fertility, he will find that ancestry does matter. That it does matter is just as good a proof of Mendelism as Mr. Darbishire's proof in the simpler case that it has not any effect. If he fails to find its influence, then he will have refuted Mendelian theory.

To illustrate my point, take a population distribution which would follow from crossing two pure races with respectively dominant and recessive characters represented by the letters D and R. Suppose the hybrids to cross at random, then the population will remain absolutely stable with the permanent formula

$$(DD)+2(DR)+(RR).$$

Now suppose this to cross with itself or with

$$(DD)+2(DR)+(RR).$$

Table I gives the scheme of offspring with their parents. This population of 16 individuals of 6 different types of parentage now crosses with itself. The result is a population of 256 individuals showing 15 types of grandparentage. This is exhibited in Table II. If Mr. Darbishire's principle that ancestry is of no importance were correct, then the differences in type of these grandparents would not be of any significance.

Table I.

Parents.	Offspring.		
	DD.	DR.	RR.
DD, DD	1	—	—
DD, DR	2	2	—
DD, RR	—	2	—
DR, DR	1	2	1
DR, RR	—	2	2
RR, RR	—	—	1

Table II.

Grandparents.					Offspring.		
DD.	DR.	RR.	+	−	DD.	DR.	RR.
4	—	—	4	—	1	—	—
3	1	—	4	—	6	2	—
3	—	1	3	1	2	2	—
2	2	—	4	—	13	10	1
2	1	1	3	1	8	14	2
2	—	2	2	2	1	4	1
1	3	—	4	—	12	16	4
1	2	1	3	1	10	28	10
1	1	2	2	2	2	14	8
1	—	3	1	3	—	2	2
—	4	—	4	—	4	8	4
—	3	1	3	1	4	16	12
—	2	2	2	2	1	10	13
—	1	3	1	3	—	2	6
—	—	4	—	4	—	—	1

Now Table II may be examined from several standpoints. We may first consider the gametic constitutions of the grandparents and of the offspring. Thus we have:—

No. of DD's in grandparentage.	Percentage of DD's in offspring.
4	100
3	67
2	41
1	22
0	11

In other words, the constitution of the grandparentage substantially modifies the offspring; there exists in this sense an "ancestral contribution" to the heritage.

Of course the gametic constitution RR follows precisely the same system of percentages, and is again influenced by ancestry.

If, however, we take the gametic constitution DR in such a population we find—

No. of DR's in grandparentage.	Percentage of DR's in offspring.
4	50
3	50
2	50
1	50
0	50

At first sight this seems to indicate that for this case there is no ancestral influence, where we should expect by increasing the number of DR's in the grandparentage to increase the number in the offspring. But this criticism is not valid, for, in the population we are dealing with, it is clear that DR is the modal or mean group, and that, accordingly, it is perfectly neutral in determining the regression or correlation of the *gametic* character. In other words, the deviations of the DR ancestry from the mean population gametic character are all zero and accordingly they have no weight in causing the offspring to deviate from the population norm. They have, in fact, no more effect on the offspring than, in the case of stature, a number of mediocre ancestors have in raising or lowering the average deviation of the offspring from the general population mean.

Lastly, turning from the gametic constitution to the somatic character, I have represented in the fourth and fifth columns of Table II the extent to which the dominant character is present in the ancestry, and in the accompanying table one sees the effect on the offspring:—

No. of grandparents with dominant character.	Percentage of offspring with dominant character.
4	89
3	78
2	59
1	33
0	0

It will thus be obvious that, judging solely by the patent, that is the somatic character of the grandparentage, there is a very marked influence of the ancestry on the heritage; that, if we select ancestry by somatic character only, we shall expect an influence on the offspring varying from 0 to 90 per cent. in intensity, according to the nature of the selection.

I think, therefore, that to deny the influence of ancestry—at any rate that influence in the sense in which the biometrician uses the term—is to deny the application of Mendelism to populations mating at random.

If we start with a population in which the proportions of DD's, DR's, and RR's are not those of a simple hybridisation, but given by

$$p\,(\mathrm{DD}) + 2q\,(\mathrm{DR}) + s\,(\mathrm{RR}),$$

then after the first generation of random mating the population will be

$$(p+2q+s)^2\,(p+q)^2\,(\mathrm{DD}) + 2\,(p+q)\,(s+q)\,(p+2q+s)^2\,(\mathrm{DR}) \\ + (p+2q+s)^2\,(s+q)^2\,(\mathrm{RR}),$$

or its constituents will be proportional to

$$(p+q)^2\,(\mathrm{DD})+2\,(p+q)\,(s+q)\,(\mathrm{DR})+(s+q)^2\,(\mathrm{RR}),$$

and this ratio is maintained ever afterwards.*

A little consideration will show that our Table II is obtained by a symbolic process which will not be affected if we replace D by $(p+q)$ D and R by $(s+q)$ R, so that to exhibit the results for a Mendelian population of any constituent proportions we have only to multiply all the numbers in any row of offspring of Table II by $(p+q)^2$ for a DD grandparent, by $(p+q)$ $(s+q)$ for a DR grandparent, and by $(s+q)^2$ for an RR grandparent, starting with the stable population which arises after the first random mating. We then reach the following table for the case of classification by somatic characters, where for brevity I write: $p+q = \pi$, $s+q = \kappa$, and $\pi^2/\kappa^2 = n =$ ratio of pure dominants to recessives in the stable population. It will be seen that whatever be the proportions of the Mendelian components in the original population, then a selection of grandparents influences widely the somatic characters of the offspring.

Whether, therefore, Mendelism be or be not the final word as to inheritance (and I personally, especially in the case of human characters, must continue to suspend my judgment), it is clear that ancestral influence cannot be denied in the case of any population mating at random and inheriting on Mendelian lines.

Table III.

No. of grandparents with dominant character.	Percentage of offspring with dominant character.
4	$100\,\dfrac{(n+1)\,(n+3)}{(n+2)^2}$
3	$100\,\dfrac{(n+1)\,(2n+5)}{2\,(n+2)^2}$
2	$100\,\dfrac{(5n+11)\,(n+1)}{6\,(n+2)^2}$
1	$100\,\dfrac{(n+1)}{2\,(n+2)}$
0	0

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* The stability after the first generation is very obvious, but, as far as I know, was first stated in print by G. H. Hardy, 'Science,' vol. 28, p. 49.

We have the following table for various values of n:—

No. of grandparents with dominant character.	Percentages of offspring with dominant character.						
	$n = 10$.	$= 4$.	$= 2$.	$= 1$.	$= \frac{1}{2}$.	$= \frac{1}{4}$.	$= \frac{1}{10}$.
4	99·3	97	94	89	84	80	77
3	95	90	84	78	72	68	65
2	78	72	66	59	54	50	48
1	46	42	37·5	33	30	28	26
0	0	0	0	0	0	0	0

When experimental work is adduced to demonstrate that ancestry has no influence, it will on investigation be found that the writer is:

(i) Confining his attention, as Mr. Darbishire, to isolated lines of inheritance, with restricted matings;

(ii) Asserting that a gametic knowledge of parents is equivalent to a gametic knowledge of ancestry.

In neither case does the argument touch the ancestral position, which is summed up in the assertions that if we measure inheritance by the resemblance of somatic characters between offspring and ancestry, then, in a population mating at random:

The more ancestors of any grade with a given somatic character the more offspring with that character.

For ancestry of different grades the influence is diminished in geometrical progression at each stage.

These principles were first deduced empirically from observations and records without any theory as to the mechanism of heredity. If Mendelism be true for any characters in cross-fertilised plants, then these principles hold also for heredity in that plant-population, for they are essential features of the Mendelian theory (and, as a matter of fact, of a good many other determinantal theories). No proof or disproof of them can be directly deduced from Mr. Darbishire's memoir, but since that memoir brings evidence for the truth of Mendelian theory, it indirectly asserts the truth that ancestry is influential, at least in the field where the biometrician expects and asserts it to play a part. This paper contains only another aspect of the results reached in 1904, but it provides in the simple case—the grandparentage—the actual percentage measures of the influence of ancestry according to Mendel. Its justification is the misinterpretation which is likely to be placed on the statement that "there is nothing like ancestral contributions within the limits of a single unit-character."*

* Darbishire, 'Roy. Soc. Proc.,' B, vol. 81, p. 71.